

**TWENTY YEARS OF FLUCTUATING PARAPATRY AND THE  
QUESTION OF COMPETITIVE EXCLUSION IN THE  
BUTTERFLIES *PONTIA OCCIDENTALIS* AND  
*P. PROTODICE* (LEPIDOPTERA: PIERIDAE)**

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*Abstract.*—The sibling species *Pontia protodice* and *P. occidentalis* occur on altitudinal gradient across the Sierra Nevada in California, with a mid-elevation belt on the west slope in which neither is a permanent resident. A similar pattern occurs in a variety of unrelated butterfly genera. Studies of the occurrence and breeding of the two *Pontia* across the Sierra for 20 years fail to demonstrate any association (positive or negative) between them in the “no man’s land” on the west slope, thus arguing against competitive exclusion as the mechanism maintaining the separation. Occurrence of *P. protodice* at 1,500 m and 2,100 m is also independent, implying that its presence in the montane Sierra is not simply an epiphenomenon of outflow from a single source in the lowlands. 1991 was an unusual year in which the entire region was colonized, seemingly in a wave emanating from the east. Sporadic competition between the species is not ruled out by these findings, but is unlikely to be important.

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Claims that “Competition from X limited the distribution of Y” used to be common in the ecological literature, but the days when they could be flung about with great abandon are over (Begon et al., 1990). That does not, however, remove the inherent seductiveness of competition-based explanations for community structure. In western North America a repeating pattern exists of altitudinally parapatric sibling species pairs (rarely triplets) of butterflies for which competitive-exclusion explanations appear attractive (Shapiro et al., 1981). In the Sierra Nevada this pattern includes *Everes comyntas* (Godart) and *E. amyntula* (Bdv.) and *L. helloides* (Bdv.) and *L. nivalis* (Bdv.) (Lycaenidae), *Phyciodes campestris* (Behr) and *P. montana* (Behr) (Nymphalidae), *Anthocharis sara* Lucas and *A. stella* (W. H. Edwards) and *Pontia protodice* (Bdv. & LeC.) and *P. occidentalis* (Reakirt) (Pieridae), *Thorybes pylades* (Scudder), *T. diversus* Bell, and *T. mexicana* (H.-S.) ssp., and *Polites sabuleti* (Bdv.) and *P. tecumseh* (Grinnell) (Hesperiidae), and others. In each case a widespread low-elevation species (the first named) is replaced in the higher Sierra by a closely-related entity of more or less ambiguous (species or subspecies) status, with a band at mid-elevation (1,300–1,700 m) in which neither occurs (or, in the *Thorybes* case, a third species occurs). Shapiro et al. (1981) were the first to point out the “natural experiment” in northern California, where the Sierran endemics *Phyciodes montana* and *Anthocharis stella* do not occur, and *P. campestris* and *A. sara* move upslope and fill more or less of the montane niches occupied by their congeners in the Sierra. This situation suggests either competitive exclusion in the Sierra or its obverse, competitive release, in the northern mountains.

Since 1972 detailed phenological data on all butterfly species have been taken along a transect parallel to Interstate Highway 80, from sea level across the Sierra Nevada

via a series of sampling stations over the crest to mid-elevation on the east slope. Each station is sampled at roughly two-week intervals in good weather whenever there is no significant snow cover; all butterfly species observed are recorded. This program is designed to permit an assessment of the spatial and temporal stability and patterning of the faunas. The data document the fluctuating parapatry across the west slope "no man's land" as well as fluctuating sympatry on the east slope in several species pairs. This paper considers the transect data on *Pontia protodice* and *P. occidentalis* and their relevance to the competitive exclusion hypothesis.

#### THE ORGANISMS

*Pontia protodice* and *P. occidentalis* are sufficiently similar morphologically to be confounded in virtually all museum and many private collections, as well as in many published works. Although Reakirt and W. H. Edwards were clear in their concepts of the species, most subsequent Lepidopterists were not. The nadir of confusion was reached by Abbott et al. (1960), who confounded *all* the North American *Pontia*, but Hovanitz (1962) mapped the distributions of *P. protodice* and *P. occidentalis* reasonably accurately, and Chang (1963) provided diagnostic morphological characters for them. Following several years of field and laboratory studies of their ecology, physiology and variation, Shapiro (1976) reviewed the status of all Nearctic names in the group and concluded that these two were amply distinct at the species level. He also concluded that the entity *nelsoni* (W. H. Edwards) from subarctic Alaska was conspecific with *occidentalis* and that both were probably conspecific with the Palearctic *P. callidice* (Hbn.) complex, which extends from the Alps and Pyrenees eastward to northeast Siberia as a series of disjunct, mostly high montane-alpine populations. According to Shapiro (*loc. cit.*): "(*Pontia*) *occidentalis* occurs upslope and northward of *P. protodice* in western North America. The two species have been found sympatric at various locations from 1000–2500m in the Rocky Mountains and Sierra Nevada, e.g., Donner Pass, California, where *P. occidentalis* is a permanent resident and *P. protodice* a breeding immigrant. . . . In areas of sympatry occasional interspecific matings may occur, but only 2 of 339 specimens collected at Donner Pass in 1973 were phenotypically ambiguous." Shapiro and Geiger (1986), using California populations including sympatric ones along the I-80 transect, demonstrated electrophoretically that they are distinct species and found no evidence for hybridization at Sierra Valley, where they are in massive contact. However, hybridization appears fairly frequent in Colorado (J. Kingsolver, D. Wiernasz, pers. comm.).

Both species occur only in non-forested environments, including tundra, grassland, high desert and steppe; *P. protodice* extends to low (hot) desert. In areas of sympatry, the two species often swarm in dense, mixed flights, breeding on weedy mustards in grain fields and by roadsides. The life cycles of both are very similar, though diagnostic differences exist in the larva and pupa (Shapiro, 1976). Both species are multivoltine (except *P. occidentalis* at the highest elevations) and feed on a variety of Cruciferae, both native and introduced. Both are highly vagile, colonizing species, and *P. occidentalis* has a "hilltopping" epigamic strategy (Shapiro 1975, 1978).

#### THE DATA

Tables 1, 2 and 4 present the occurrence of both species at the Sierran stations along the I-80 transect: Lang Crossing, Nevada Co.,  $\pm 1,500$  m (LC); Donner Pass,

Table 1. Occurrence and breeding of *Pontia protodice* at Lang Crossing (LC), Donner Pass (DP), and Castle Peak (CP), 1972–1991.

Year	LC (1,500 m)		DP (2,100 m)	CP (2,700 m)
1972 <sup>a</sup>	1♀, x.4		1♂, 2♀, ix.7	—
1973	—		1♂, vi.27, through ix.28, BRED	—
1974	1♀, ix.25		—	—
1975	—		2♂, ix.13; 1♀, ix.25	—
1976	1♂, viii.13		1♂, viii.20, through xi.20, BRED	—
1977	1♀, iv.17		1♂, iv.22	—
	1♀, vi.15, through x.20, BRED		3♂, vii.1, through x.13, BRED	
1978	1♀, vi.9, through xi.5, BRED		1♂, ix.12; 1♀, x.27	—
1979	1♂, viii.19; 1♀, viii.30		—	—
1980	1♂, 2♀, viii.4, through x.6, BRED		2♀, ix.27; 1♂, x.10	—
1981	—		1♂, viii.31; 1♀, ix.6; 1♀, ix.12	—
1982	—		2♀, ix.1	—
1983	1♀, vi.5; 1♀, ix.12		1♂, 1♀, ix.14; 1♀, ix.28	—
1984	—		3♀, vii.20; 1♂, x.10	—
1985	1♀, vi.24; 1♂, viii.13		4♂, 2♀, vi.19, through ix.4, BRED	—
1986	1♂, 1♀, vi.10		1 larva, vii.18	1♀, viii.26
1987	1♂, 1♀, vii.20		—	—
1988	2♂, 1♀, vi.16, through x.12, BRED		3♂, 1♀, viii.31, through x.8, BRED	1♀, vii.9; 2♂, ix.10
1989	1♀, ix.23		2♂, 1♀, viii.14; 1♂, viii.15	—
1990	1♂, ix.5; 1♀, x.12		5♂, 3♀, vii.19, through ix.28, BRED	—
1991	2♂, vii.28, through ix.20, BRED		1♂, vi.21, through x.5, BRED	1♂, 1♀, vii.3; 1♀, viii.2

<sup>a</sup> Sampling stations were moved a few km in 1973 and remained in their new sites thereafter.



Table 2. Occurrence and breeding of *Pontia occidentalis* at Lang Crossing (LC), 1972–1991. This species has been present and breeding in all years at DP and CP.

Year	LC (1,500 m)
1972	—
1973	—
1974	—
1975	1♀, viii.13
1976	—
1977	1♀, iv.17 <sup>a</sup>
1978	2♂, 1♀, viii.17; 1♂, ix.14; 1♀, x.6; BRED
1979	—
1980	2♀, vii.14; 1♂, viii.4 <sup>b</sup> ; 10♂, 3♀, viii.26; 1♂, ix.10; BRED
1981	—
1982	—
1983	1♀, ix.12
1984	—
1985	—
1986	—
1987	1♂, 1♀, vii.20; 1♂, ix.7; BRED
1988	1♀, vii.22
1989	1♀, vi.22; 1♀, vii.17; 1♀, viii.5; 1♂, viii.16; BRED
1990	—
1991	—

<sup>a</sup> Implies colonization and overwintering undetected in 1976.  
<sup>b</sup> Apparent hybrid.

Nevada and Placer Cos., ±2,100 m (DP); Castle Peak, Nevada Co., ±2,700 m (CP); and Sierra Valley, Sierra Co., ±1,500 m (SV). Lang Crossing is a west-slope locality with a mosaic of mixed mesic forest, montane chaparral and Canyon Live Oak xeric woodland on metasedimentary balds, and wet and dry meadows. Donner Pass contains mostly upper montane coniferous forest on a mixture of granite and andesite substrates, but is penetrated by a large wet and dry meadow complex and disturbed roadsides and railway rights-of-way which extend completely through the pass, from one slope to the other; these are lined with Crucifers. Castle Peak (Shapiro, 1978) has subalpine coniferous forest and dry alpine fell-fields on andesite. Sierra Valley is a very large wet and dry meadow complex on Pleistocene lake alluvium, with some alfalfa cultivation along the margins. It is hemmed in by coniferous forest to the west (on the east face of the Sierra) and by a low range of volcanic hills to the east, historically covered with open pine forest but now occupied by sagebrush steppe and juniper woodland; beyond these hills lies the Great Basin high desert.

LC and DP have been sampled for 20 years (the sampling stations were moved several km from their 1972 locations to permanent ones in 1973). CP has been sampled for 20 years, but only 4–6 times/year due to its short flight season. SV was sampled sporadically before 1980 and systematically thereafter, but early-spring data (including the very early flight periods of post-diapause *Pontia*) were obtained only since 1985.

Host plants recorded at the transect stations are presented in Table 5.

Table 3. Dates of first records of *Pontia protodice* at Sierra Valley (SV), where the species is apparently always present in summer. In 1988 and 1990 the first (overwintered) brood, “*vernalis*,” was recorded in April, and the second date corresponds to other years as the beginning of the summer flight.

Year	First date
1985	vi.20
1986	vii.11
1987	vii.1
1988	iv.14; vi.19
1989	vi.3
1990	iv.12; vii.7
1991	vi.13

The data are divided into “occurrence” and “breeding” years. Unavoidably, this classification is somewhat arbitrary; deciding whether or not breeding has occurred is sometimes not easy. Multiple captures on the same day at the same site are not necessarily indicative of local origin (see discussion of dispersal, below). Interpretation of the data involves: consideration of timing and previous frequency, and intervals of sampling; numbers, condition, and sex-ratio of the animals observed; and appropriateness of phenotype relative to season, both locally and in potential source areas (both species are seasonally polyphenic). By these criteria many multiple records have been interpreted as evidence of immigration rather than breeding from a previously undetected colonist. The reality of undetected colonists, however, is underscored by the discovery on 18 July 1986 of a large larva of *P. protodice* at DP in a year when no adults of that species were seen there. For all years in which breeding is claimed in the tables, the numbers and sexes of adults seen at the first observation are noted. Criteria for recognizing breeding include: direct observation of oviposition and/or early stages; ongoing (essentially continuous) presence of adults over several consecutive samples; presence of newly-emerged or teneral individuals; and appearance of two or more consecutive emergences at intervals appropriate for successive generations *in situ*.

Table 4. Status of both species at all four sites, as fractions of years present or breeding (1986 was not treated as a breeding year for *P. protodice* at DP). For criteria used to assess breeding, see text.

	LC	DP	CP	SV
Occurrence				
<i>P. protodice</i>	15/20	16/20	3/20	10/10
<i>P. occidentalis</i>	8/20	20/20	20/20	10/10
Breeding				
<i>P. protodice</i>	5/20	7/20	0/20	10/10
<i>P. occidentalis</i>	4/20	20/20	20/20	10/10

Table 5. Hosts (all Cruciferae) recorded for *Pontia protodice* (P) and *P. occidentalis* (O) at LC, DP and SV, 1972–1991. Additional hosts occur for O at CP.

	LC	DP	SV
<i>Lepidium virginicum</i> var. <i>pubescens</i> (Greene) Thell.	P, O	P, O	P, O
<i>Lepidium perfoliatum</i> L.			P, O
<i>Sisymbrium altissimum</i> L.	P, O		P, O
<i>Descurainia sophia</i> (L.) Webb		P, O	P, O
<i>Descurainia pinnata</i> (Walt.) Brit.			P, O
<i>Cradaria pubescens</i> (Mey.) Roll.		P, O	P, O
<i>Streptanthus tortuosus</i> Kell.	O	O	

RESULTS

*Pontia occidentalis* is a permanent resident at DP, CP and SV. This is shown by the predictable occurrence of the vernal, post-diapause brood “*calyce* (W. H. Edwards)” (Shapiro, 1976) shortly after snowmelt, though it flies so early it is easily missed. This is not the case at LC, and it very rarely overwinters there.

*Pontia protodice* is not a permanent resident at LC, DP or CP. Its status at SV is uncertain. It has been common or abundant there in summer, with 2–3 generations, every year for nearly 20 years, but early spring data are only available for seven years and in only two of these was the vernal, post-diapause brood “*vernalis* (W.H. Edwards)” (Shapiro, 1976) observed (Table 3). In the Nevada desert and on the floor of the Sacramento Valley (Shapiro, 1979 and unpublished), *P. protodice* overwinters only locally and sporadically. Failure to detect it in early spring in Sierra Valley may not establish its status in a broader, regional context.

Upslope movement by *P. protodice* on a seasonal basis is strongly supported by circumstantial evidence. In 1991, for example, no *protodice* were seen at SV through 1 June. On 13 June, however, they were abundant and uniformly worn and of the second-brood phenotype that was flying at that time around Reno. Females oviposited on roadside Crucifers. Given the climatic and vegetational differences between Reno

Table 6. Comparisons of observed and (in parentheses) expected frequencies of *P. protodice* (P) and *P. occidentalis* (O) alone and in combination at LC, 1972–1991. Neither distribution differs statistically from mutual independence (unadjusted  $\chi^2$  values;  $\chi^2$  adjusted for continuity also NS).

	P +	P –
Occurrence		
O +	7 (6)	1 (2)
O –	- 8 (9)	4 (3)
	$\chi^2 = 1.055$ , NS	
Breeding		
O +	2 (1)	2 (3)
O –	3 (4)	13 (12)
	$\chi^2 = 1.67$ , NS	



Table 7. Comparisons of observed and (in parentheses) expected frequencies of occurrence and breeding of *P. protodice* at LC vs. DP. (These are unadjusted  $\chi^2$ ; adjusted  $\chi^2$  are NS for both comparisons,  $\chi^2_{\text{adjbreeding}} = 1.18$ .)

	LC +	LC -
Occurrence		
DP +	12 (12.75)	5 (4.25)
DP -	3 (2.25)	0 (0.75)
	$\chi^2 = 1.54$ , NS	
Breeding		
DP +	3 (1.50)	3 (4.50)
DP -	2 (3.50)	12 (10.50)
	$\chi^2 = 2.96$ , .05 < $P$ < .10	

and SV, this apparent synchronization is unlikely to be coincidental. On 21 June a male of this phenotype, in poor condition, was taken at DP. On 18 June both sexes were common between Gardnerville, NV and Woodfords, Alpine Co., CA and along the Kingsbury Grade highway to South Lake Tahoe, where they were flying upslope along the roadside. This sort of movement seems to occur every year, albeit usually less conspicuously, and could account for the abundance and reliable occurrence of *P. protodice* at SV each year without overwintering.

What can 20 years of occurrence and breeding data along our transect tell us? Given that neither species persists at LC, that site is particularly important as a potential indicator of competitive exclusion: is the occurrence of the two species either positively or negatively correlated? A negative association could imply either competitive exclusion or reciprocal conditions for colonization (without regard to competition—for example, wet years might favor one species, dry years the other). A positive association would argue against competitive exclusion, suggesting that the same conditions favor colonization by both. There is a single remarkable record of a long-range dispersal by *P. occidentalis*, resulting in its capture in prime *P. protodice* habitat near sea level (Shapiro, 1977)—suggesting that the two species have similar habitat preferences as expressed in active habitat selection.

Table 6 shows that both occurrence and breeding data do not differ significantly from the values expected if the two species were completely independent.

Also of interest is the extent to which occurrence and breeding of the two species are linked among LC, DP and CP. If occurrence at these sites is an epiphenomenon of dispersal from a uniform source (either east or west of the Sierra) we would expect a strong association, while colonization from both sides would produce much weaker association unless population densities in both potential source regions were tightly coupled. Table 7 does not indicate strong association among sites. Mere occurrence is indistinguishable from independence between LC and DP, while the hint of association for breeding is entirely due to 1991 (and disappears if that year is not considered). 1991 was in fact a very unusual year for *P. protodice*. As Table 1 indicates, it did eventually show up at LC and breed there. But it continued spreading westward into the lower foothills, where it merged with an already established population in

the Sacramento Valley; 1991 was the first year since 1977 in which *P. protodice* spread very widely (it reached the Oregon border in Modoc and Siskiyou Counties) and the only year in the history of the transect that it occurred at all ten stations. *P. protodice* is so rare at CP (Table 1) that no analysis is feasible, or necessary, beyond noting that 1988 and 1991 were breeding years at DP, while 1986 was marked by only the single larva mentioned above.

These data thus give no support to competitive exclusion as the cause of either the "no man's land" on the Sierran west slope or the altitudinal stratification of *Pontia* overall. It must be stressed that the sort of comparison done here is not powerful enough to detect competition itself; it can only be suggestive. Nor do these results rule out the possibility of local competition arising as a consequence of the spatial pattern of egg dispersion on hosts (Shapiro, 1975), with no larger-scale impact on distribution.

As Begon et al. (1990) point out, it may not be possible to exclude *prior* competition and character displacement as factors leading to contemporary patterns of replacement or apparent exclusion. Unless that hypothesis is testable, however, it is not very interesting. Altitudinal parapatry is a common pattern in a variety of organisms. In the tropical Andes much more complex patterns can be found in butterflies than occur in the Sierra Nevada (Adams, 1973). Because these patterns could be involved in the process of speciation, it is important to understand how they are maintained; so far there is no persuasive evidence that competition is involved—in *Pontia* or otherwise.

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